Journal of Applied Ecology

British Ecological Society

Journal of Applied Ecology 2010, **47**, 524–531 doi: 10.1111/j.1365-2664.2010.01805.x

Evaluating the Canada lynx reintroduction programme in Colorado: patterns in mortality

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Summary

1. Reintroducing carnivores has become a widely used technique to restore the natural integrity of ecosystems. Accurate estimates of demographic parameters for reintroduced populations are essential to evaluate the success of the reintroduction programme, assess the need to release additional animals and to develop management recommendations.

2. In an effort to establish a viable population of Canada lynx *Lynx canadensis* in Colorado, USA, the Colorado Division of Wildlife released 218 wild-caught lynx from 1999 to 2006. All lynx were released with very high frequency (VHF) and/or satellite transmitters from which locations, mortality, reproduction, habitat use and movement patterns were documented. We present estimates of mortality.

3. Known-fate models could not be applied here to estimate mortality due to excessive missing location data because of either extensive movement outside of the study area or transmitter failure. Instead we employed a multistate model to address these issues.

4. We describe how the more general multistate mark–recapture model can accommodate missing data to estimate monthly mortality rates of released lynx both inside and outside the study area. We also explored factors possibly affecting lynx survival such as sex, time spent in pre-release captivity, movement patterns and origin.

5. Monthly mortality rate was lower inside the study area than outside, and slightly higher for males than for females, although 95% confidence intervals overlapped for sexes. Mortality was higher immediately after release [first month = 0·0368 (SE = 0·0140), and 0·1012 (SE = 0·0359) respectively, inside and outside the study area], and then decreased according to a quadratic trend. Annual survival was 0·9315 (SE = 0·0325) within the study area and 0·8219 (SE = 0·0744) outside the study area.

6. *Synthesis and applications.* For those contemplating lynx, or other carnivore reintroductions, we suggest identifying a high-quality release site to minimize mortality. We recommend that managers consider the demography of animals separately within and outside the reintroduction area for valid assessment of the reintroduction. Movements of reintroduced animals and their subsequent loss through death or permanent emigration may require the need for additional individuals to be released for a successful reintroduction effort.

Key-words: Canada lynx, carnivore, Colorado, known-fate model, *Lynx canadensis,* mortality, multistate model, program MARK, reintroduction, telemetry

Introduction

Carnivores have been eliminated from many ecosystems all over the world. Reintroduction of locally extirpated populations has become a common tool for conservation and management of wildlife species (van Wieren 2006). Carnivore reintroductions, in particular, can be viewed as a step towards restoring the natural integrity of ecosystems (Noss *et al.* 1996; Miller *et al.* 1999) because carnivores alter the structure and function of ecosystems via predation and interspecific competition (Terborgh *et al.* 2001). Yet, the reintroduction of endangered carnivores is controversial and as much a political as a

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biological challenge (Treves & Karanth 2003). Biologically, large carnivores seem particularly difficult to reintroduce (Miller *et al.* 1999) because their extensive habitat requirements often result in conflicts with human activities (Bixby 1992; Treves & Karanth 2003). Politically, individuals from different professional, organizational, geographical or economic groups have different perspectives on the reintroduction of carnivores (Clark, Curlee & Reading 1996; Primm & Clark 1996). Divergent views can lead to conflicts between preservation vs. use of resources, recreation-based vs. extraction-based economies, or urban vs. rural values (Kellert *et al.* 1996; Rasker & Hackman 1996).

Despite these hurdles, several reintroductions of carnivores have been conducted such as the Eurasian lynx *Lynx lynx* to the Alps (Breitenmoser & Brietenmoser-Würsten 1990); the black-footed ferret *Mustela nigripes* to the central prairies of the United States (Dobson & Lyles 2000); or the grey wolf *Canis lupus* to Yellowstone National Park (Fritts *et al.* 1997). Evaluation of such programmes is critical for providing evidence to decide whether or not such efforts should be continued, and to improve efficacy of large carnivore reintroductions. In this paper, we focus on evaluating the mortality of Canada lynx *Lynx canadensis* reintroduced to CO, USA.

Canada lynx historically occurred throughout the boreal and western montane cordilleran (Brandt 2009) forests of North America. Lynx populations in Alaska and Canada vary with snowshoe hare *Lepus americanus* densities, but are considered persistent and robust to these natural fluctuations (Blasius, Huppert & Stone 1999). However, the species is currently listed as threatened in the contiguous United States under the Endangered Species Act (ESA) of 1973, as amended (16 U.S.C 1531 et seq.; US Fish and Wildlife Service 2000). Colorado represents the southern-most historical distribution of Canada lynx, where the species occupied the higher elevation montane forests. Lynx were essentially extirpated from the state by the late 1970s, due to unregulated trapping, predator control and habitat incursion (Meaney 2002). Given the isolation of Colorado to the nearest northern populations, the Colorado Division of Wildlife (CDOW) considered reintroduction as the only option to re-establish the species in the state, and initiated a reintroduction programme in 1997 (Seidel *et al.* 1998). From 1999 to 2006, 218 wild-caught lynx from Alaska and Canada were released in south-western Colorado (Shenk 2009). This constitutes the largest Canada south-western lynx and, possibly, meso-carnivore reintroduction effort to date.

The goal of the Colorado lynx reintroduction programme is to establish a self-sustaining, viable population of lynx in the state. As Canada lynx is a relatively long-lived species, adult survival plays a key role in their population dynamics (Dobson & Oli 2007). Therefore, one important goal of the post-release monitoring was to estimate mortality of the re-introduced lynx, and where possible, to determine the causes of death. Additional questions existed concerning survival of the reintroduced lynx. Was survival higher within the reintroduction area than outside the area? Did survival vary by sex, the amount of time spent in pre-release captivity, the place of origin, year/season of release or reproductive status? Such information will be used to assess the success of the reintroduction programme, and possibly to improve future reintroductions.

All lynx released in Colorado were equipped with very high frequency (VHF) and/or satellite transmitters to provide biweekly locations. Although mortality rates are often obtained from such telemetry data using known-fate or nest-survival models (White & Garrott 1990; Schwartz *et al.* 2006), these approaches could not be applied here because of excessive missing data, which led to violating the key assumptions that detection equals 1 and fates are known. Regular location data were not always obtained for all individuals due to logistical constraints of the aerial survey, extensive movements of lynx outside of the study area, or transmitter failure. We briefly describe how the multistate mark–recapture models (Brownie *et al.* 1993; Lebreton & Pradel 2002) could be applied, despite missing data, to estimate monthly mortality rates of released lynx. Our results are specifically relevant to evaluating this Canada lynx reintroduction, but may also be useful for other planned carnivore reintroductions. Our methodological approach should be useful in analysing data from other telemetry studies where the assumption of known fate cannot be met, which we believe is often the case.

Materials and methods

STUDY AREA AND STUDY ANIMALS

Byrne (1998) evaluated five areas within Colorado as potential lynx habitat based on: (i) snowshoe hare density (Bartmann & Byrne 2001); (ii) road density; (iii) area size; (iv) juxtaposition of habitats within the area; (v) historical records of lynx observations and (vi) public issues. Based on these results, the San Juan Mountains of south-western Colorado were selected as the reintroduction area. Wild Canada lynx were captured in Alaska, British Columbia, Manitoba, Quebec and Yukon (Table 1), and transported to the reintroduction area in Colorado where they were first held at a rehabilitation facility and then released within 40 km of the Rio Grande Reservoir.

We focused post-release monitoring efforts on a 20 684 km^2 study area including the reintroduction area and contiguous, surrounding high elevation sites (>2591 m). The area encompassed the south-west quadrant of Colorado and was bounded on the south by New Mexico, on the west by Utah, on the north by Colorado Highway 50, and on the east by the Sangre de Cristo Mountains (Fig. 1). South-western Colorado is characterized by wide plateaus, river valleys, and rugged mountains reaching over 4,200 m. Within the study area, the most widely distributed coniferous forest type is composed of Engelmann spruce *Picea engelmannii* and subalpine fir *Abies lasiocarpa*.

TELEMETRY COLLARS AND SAMPLING ISSUES

To monitor lynx movements, released individuals were fitted with telemetry collars. All lynx released in 1999 were fitted with Telonics^{TM} (Mesa, AZ, USA) radiocollars. Except for five males released in spring 2000, all lynx released after 1999 were fitted with Sirtrack^{TM} (Havelock North, New Zealand) dual satellite/VHF radiocollars. The satellite collar's platform transmitter terminal (PTT) was programmed to be active for 12 hours per week, and locations were obtained via Argos, National Aeronautics and Space Administration (NASA), and National Oceanic and Atmospheric Administration (NOAA) satellites.

Table 1. Number of wild-caught male (M) and female (F) Canada lynx *Lynx canadensis* from Alaska (AK) and Canada (BC = British Columbia, MB = Manitoba, QU = Quebec and YK = Yukon) released in south-western Colorado from 1999 to 2006

			State/Province of Origin					
Year	% released	Sex	AK	BC	MB	QU	YK	Total
1999	19	F	13	5			4	22
		M	7	6			6	19
2000	25	F	6	9			20	35
		M	4	9			7	20
2003	15	F		10		7		17
		M		10	1	5		16
2004	17	F		7		10		17
		M		13		7		20
2005	17	F		4	3	8	3	18
		M		9		8	3	20
2006	6	F		4			3	7
		M		5			2	7
Total			30	91	4	45	48	218

Once activated, satellite transmitters (PTT) provided weekly locations at the continental scale without further human intervention or bias. Aeroplane flights were conducted weekly over the study area (Fig. 1) to obtain lynx locations using VHF telemetry, depending on weather and availability of planes and pilots. During the den search season (15may–30June), two flights per week were conducted to locate VHF-equipped animals throughout Colorado and in the border areas of Wyoming and New Mexico where contiguous montane habitat occurred. VHF location data were also collected intermittently outside the study area during CDOW management activities. Accuracy of aerial locations (VHF) ranged from 50 to 500 m, and accuracy of satellite location (PTT) ranged from 0·15 to 10 km. We assumed a random error direction in the locations and used the point location to determine if a lynx was on or off the study area.

Due to these different data collection procedures, the detection probability of a PTT signal was always close to 1, whereas that of a VHF signal was close to 1 within the study area only, and dropped to < 1 where flights could not be conducted as regularly. In addition, the batteries of PTT and VHF transmitters lasted approximately 1·5 and 5 years, respectively. Hence, outside the study area, the detection probability was ~ 1 as long as the PTT transmitter was active but dropped to < 1 once the PTT battery died.

Whenever possible, lynx with a failed transmitter (PTT, VHF or both) were captured, re-collared with a new dual PTT/VHF transmitter collar and re-released immediately. However, some individuals ($n = 13$) were held in captivity because they were in poor body condition, wounded, or because they were recaptured in atypical habitat and were re-released within the reintroduction area. For these individuals, we censored the data by discarding all encounters occurring after the recapture date to eliminate any effect of an additional captivity on mortality.

When a mortality signal was detected, the location was recorded, and ground crews located and retrieved the carcass as soon as possible (generally within 3 weeks), and searched the immediate area for evidence of cause of death. Carcasses were transported to the Colorado State University Veterinary Teaching Hospital (Fort Collins, CO, USA) for a post-mortem examination and if possible, determination of the cause of death.

As little information was available on successful release protocols for Canada lynx, the release protocol was first investigated by trial and error in 1999. Early release protocols led to death by starvation for four (out of 13) of the first reintroduced lynx, and caused controversy about the reintroduction programme (Kloor 1999). The release protocol was altered after these first deaths and applied to all the subsequently released lynx. The final protocol called for releasing adults only (non-pregnant for females), in the spring, after at least 3 weeks

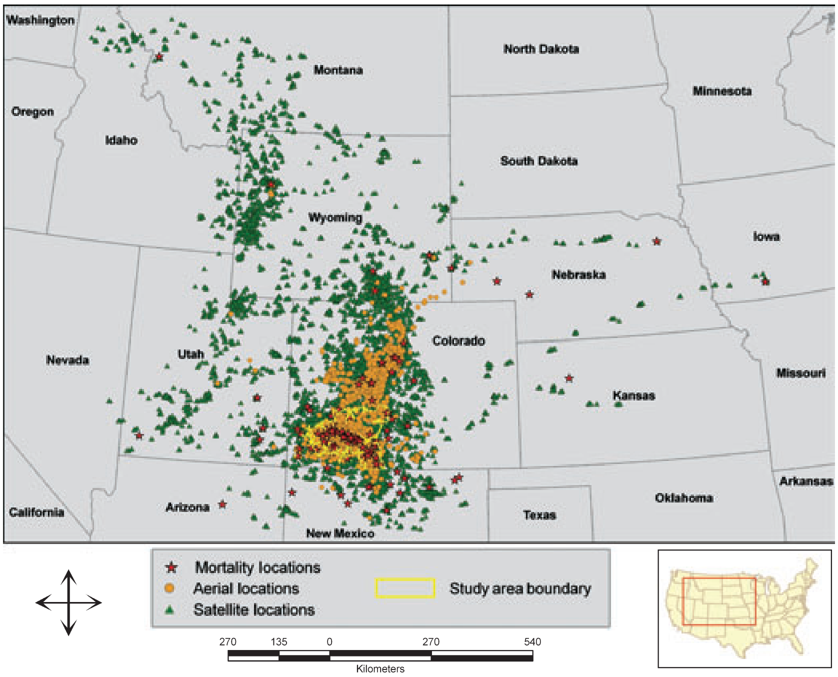

Fig. 1. Map of Colorado outlining the core reintroduction and primary post-release monitoring area, and documenting all post-release locations obtained by either satellite platform transmitter terminal or aerial very high frequency tracking for the 218 lynx reintroduced to Colorado from February 1999 to November 2007. All known mortality locations are shown as stars.

in the holding facility, where they were fed a high quality diet (Shenk 2000; O. Devineau *et al.* Unpublished data). Spring release would assure the highest annual abundance of prey in the reintroduction area and releasing animals after the lynx breeding season (March and April) eliminated the complication of reproduction for newly released lynx. Pre-release captivity encouraged recovery from the stress of capture and transport as well as weight gain for most lynx (Wild 1999), thus allowing a better body condition at the time of release.

MODELLING FRAMEWORK AND MODEL SET

Because of the vagaries of VHF survey flights, movements of lynx, transmitter failures and difficult access to mountainous terrain, our data did not meet the main assumptions of a typical telemetry/known-fate study: that detection probability (*P*) always equalled 1, and that all fates (dead or alive) were known (White & Garrott 1990). To address this issue, we employed a multistate model (Brownie *et al.* 1993; Lebreton & Pradel 2002; Lebreton *et al.* 2009) as implemented in program MARK (White & Burnham 1999).

We considered our encounter data as being in one of four states: a lynx could be detected alive inside the study area (state I), alive elsewhere (state E), dead inside the study area (state i) or dead elsewhere (state e; Fig. 2). Occasions before initial release and after last detection were coded as '.' (period), and were ignored by program MARK. When lynx were searched for but not detected, the corresponding occasion was coded as 0 (zero). Data were collapsed to 1-month intervals, using only the first encounter from each month. Each encounter history was assigned to one of two groups: (i) 'VHF-only' when no PTT transmitter was present or when the PTT transmitter had failed leaving only the VHF transmitter active; or (ii) 'PTT' when a working PTT transmitter was present.

Multistate models provide three types of parameters: detection, survival and transition probabilities (Lebreton *et al.* 2009). We estimated detection probabilities directly for each type of transmitter

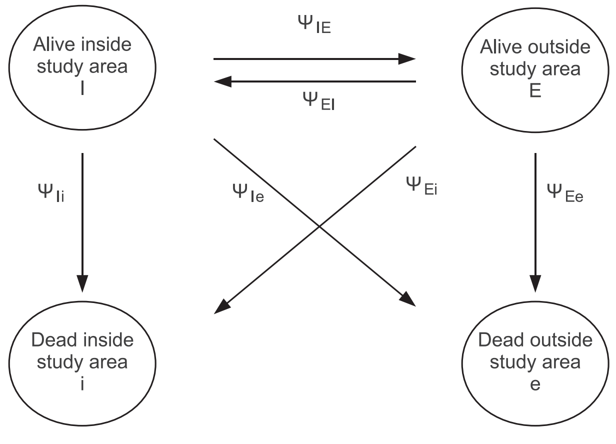

Fig. 2. Depiction of the multistate model used for the analysis. Individual lynx were in one of four states (alive inside the study area, I; alive outside the study area, E; dead inside the study area, i; dead outside of the study area, e). Individuals could transition according to the arrows, and other transitions (not shown) were not possible, thus fixed to zero. Since transitions from alive to dead states were mortality rates, survival probabilities (self loops) for all states were fixed to 1. Detection probabilities were modelled for each state depending on whether the lynx had an active platform transmitter terminal and/or very high frequency transmitter. Although transitions are independent of each other on this diagram, we modelled transitions $\hat{\psi}_{Ie}$ and $\hat{\psi}_{Ei}$ as a combination of the other movement and mortality parameters such that $\hat{\psi}_{Ie} = \hat{\psi}_{IE}\hat{\psi}_{Ee}$ and $\hat{\psi}_{Ei} = \hat{\psi}_{EI}\hat{\psi}_{Ii}$.

and for inside and outside the study area. Although the detection probability of an active PTT transmitter should be equal to 1, we estimated it directly. Detection probabilities of PTT-equipped lynx were considered equal for all four states (I, E, i, e), whereas those for VHF-only equipped lynx were estimated separately for each state. However, due to insufficient data, the probability of detecting a VHF-only equipped lynx inside the study area was forced equal for live and dead lynx. Given monitoring efforts were continuous through time, we held detection probabilities constant over time in all models.

Transitioning from one state to another over a time interval implies surviving over (or dying in) that interval and the actual movement on or off the study area. Hence, mortality rates can be estimated using either the survival or the mortality-transition parameters of the multistate model. We fixed survival parameters to 1, and relied upon transitions parameters to model both mortality and movement of lynx (Figs 1 and 2). We estimated movement rate from inside to outside the study area ($\hat{\psi}_{IE}$) separately from movement from outside to inside the study area ($\hat{\psi}_{EI}$). Due to limited sample size and expected low movement rates, we modelled these movements as constant over time. We modelled mortality as the transition probabilities ($\hat{\psi}$) from live states (I, E) to dead states (i, e). As dead states (i, e) were absorbing states (i.e. impossible to transition from), transition probabilities from dead states to live states were fixed to 0 (Fig. 2). We modelled transitions from alive inside to dead elsewhere ($\hat{\psi}_{Ie}$) and from alive elsewhere to dead inside ($\hat{\psi}_{Ei}$) as a combination of the other movement and mortality parameters such that $\hat{\psi}_{Ei} = \hat{\psi}_{EI}\hat{\psi}_{Ii}$. This structure required the use of a log link function for all transition parameters in the likelihood equation.

Based on Byrne's (1998) results, we assumed the study area offered the most contiguous high quality lynx habitat in Colorado, and that lynx outside the study area would encounter a mixture of interspersed high and low quality habitat and have higher travel and road encounter rates. Therefore, we hypothesized that lynx mortality would be higher outside the study area than inside, which formed our base model.

Based on the biology of lynx and on the outcomes of initial release protocols, we considered various individual and time-varying covariates. Because lynx were captured in different boreal forests of Alaska and Canada, and released into the montane forests of Colorado, we tested whether the origin of released lynx (ORIGIN) had an impact on post-release mortality. To account for behavioural differences between males and females and for seasonal differences in release protocols, we considered the effects of sex (SEX) and of season of release (RELSEAS, i.e. winter/spring). We also tested models including total time in pre-release captivity (DCAPTIV), from the date of first capture in the wild to release in Colorado (range 12–151, mean = 87 days, SE = 2·6). Too few days in captivity may not be sufficient for recovery between capture and transport, weight gain or acclimation to the release area. Alternatively, extended captivity may lead lynx to associate food with humans or to be fearless of humans, thus resulting in more contacts with humans and possibly higher mortality. Finally, we considered the effect of year of release (RELYR). In particular, we modelled 1999, and 1999–2000 differently from subsequent years to account for the initial phase of trial and error with the release protocols. We also hypothesized that lynx released in the first year of the reintroduction, 1999, would have higher mortality due to their higher dispersal rates (km travelled per month; T. M. Shenk, unpublished data), possibly in response to the lack of conspecifics in the study area. We also considered the reproductive status (REPRO) as a time-varying covariate. Female lynx were considered reproductive when accompanied by dependent kittens (up to 10 months old). A male was considered reproductive if he remained in the same area as a reproductive female.

Due to the effect of the reintroduction itself we thought mortality might be highest right after release, but then decrease as lynx became familiar with the area. Similarly, mortality could increase again after some time due to age or to increased intraspecific competition due to more lynx being born or having been released. We modelled this hypothesized relationship between mortality and time since release as a linear trend (LINTREND), and as a quadratic trend (QUADTREND), as well as with a threshold model in which mortality declined before being forced constant (THRESHOLD). Each variable was considered singly and in additive combinations, though data sparseness prevented us from creating the full model. We used Akaike's Information Criteria with small sample size correction (AIC_c; Burnham & Anderson 2002) for model selection. In addition, to monthly mortality estimates, we provide estimates of annual survival as they may be more intuitive. These annual estimates were calculated by raising the monthly survival for the 50th month after release (i.e. once mortality was stabilized) to the power 12. We used the delta method to calculate the associated standard errors.

Results

Between 1999 and 2006, 218 lynx (115 females, 103 males) were released. The initial lynx released in 1999 and 2000 were monitored through 2001 and 2002 to determine fates before releasing additional individuals: no lynx were released in 2001 and 2002 (Table 1). Following this evaluation, additional lynx were released in 2003–2006. By 1 November, 2007, 9991 good quality satellite locations (accuracy of 0–1000 m) and 9942 VHF locations (Fig. 1) had been obtained. Collapsing the data to a single monthly location per individual yielded 9977 locations for the analysis. Of the 218 lynx released, 41 were never detected outside the study area, either because they never left the study area, died shortly after release, or because they were equipped with a VHF-only transmitter and had a lower probability of being detected outside the study area. We detected 177 lynx at least once outside the study area; among those, 63 were detected more often outside the study area than inside, 152 were detected more frequently within the study area than outside, and three individuals were detected equally frequently on and off the study area.

By November 2007, 101 (47%, 57 females, 44 males) of the reintroduced lynx had died. Although 36% of deaths could not be attributed to any particular cause, the main known causes of mortality were gunshot, vehicle collision and starvation (Table 2). Mortalities occurred both on (44%) and off (56%) the study area (Fig. 1). All top models included the quadratic trend over time (QUADTREND), and the minimum-AIC_c model also included the effect of release year (RELYR). This model accounted for 53% of the AIC_c weight (Table 3, Fig. 3). The effect of release year (RELYR) and number of days in pre-release captivity (DCAPTIV) were also present in the top ranking models. However, the release year effect was weak with only 2003 and 2004 being slightly different from the other years [Beta values: 2003: −1·317, CI (−2·330, −0·304), 2004: −0·984, CI (−1·868, −0·100)]. Similarly, the number of days in captivity [Beta value from second best-AIC_c model: −0·008, CI (−0·014, 0·003)] had little explanatory ability.

As model structure for detection probabilities was the same across models, we report only estimates from the best-AIC_c model. Within the study area, the monthly probability to detect a live or dead lynx with a VHF-only transmitter was 0·8400 (SE = 0·0107). Outside the study area, the probability to detect a VHF-only lynx was 0·5369 (SE = 0·0198) for live individuals and 0·1888 (SE = 0·0338) for dead individuals. The probability of an individual returning to the study area was slightly higher (0·0922, SE = 0·0072) than for an individual to leave the area (0·0712, SE = 0·0045). Monthly mortality was low, even immediately after release (Fig. 3). For the first month after release, mortality was 0·0368 (SE = 0·0140) inside, and 0·1012 (SE = 0·0493) outside the study area. Given monthly mortality levelled off by the 50th month following release, we used the estimate for the 50th month to calculate the annual survival. Annual probability of survival was 0·9315 (SE = 0·0325) within the study area and 0·8219 (SE = 0·0744) outside the study area.

Table 2. Cause of death and number of female (F), male (M), and sex unknown (U) Canada lynx *Lynx canadensis* found dead, both inside and outside the study area in south-western Colorado, from 4 February 1999 – 1 November 1 2007

	Inside		Outside				
Cause of Death	F	M	F	M	U	Total	%
Illness			1	1		2	2
Predation		2		1		3	3
Probable predation			3			3	3
Plague	5	1		1		7	7
Other trauma	1	2	3	2		8	8
Starvation	5	3	2			10	10
Hit by vehicle	3	1	5	3	1	13	13
Shot	1	5	5	3		14	14
Probable shot	3	1		1		5	5
Unknown	7	5	13	12		37	36
Total	25	20	32	24	1	102	

Table 3. Models for transition parameters for which AIC_c model weights were > 0·001. For all models, detection probabilities were considered constant over time, and estimated separately for Very high frequency- and Platform transmitter terminal-transmitters and for inside and outside of the study area. Survival parameters were fixed to 1, and impossible transitions (e.g. from dead to live) were fixed to 0. Transition parameters were used to estimate both movement on and off the study area (separately but constant over time), and mortality rates. Transitions $\hat{\psi}_{Ie}$ and $\hat{\psi}_{Ei}$ were considered dependent of other movements ($\hat{\psi}_{IE}$,$\hat{\psi}_{EI}$) or mortality ($\hat{\psi}_{Ii}$,$\hat{\psi}_{Ee}$) transitions, such that $\hat{\psi}_{Ie} = \hat{\psi}_{IE}\hat{\psi}_{Ee}$ and $\hat{\psi}_{Ei} = \hat{\psi}_{EI}\hat{\psi}_{Ii}$. QUADTREND: quadratic trend, i.e. mortality decreases over time since release; RELYR: year of release; DCAPTIV: number of days in captivity before release; REPRO: reproductive status

Model	ΔAIC_c	AIC_c weight	Likelihood	#par
QUADTREND + RELYR	0·00	0·816	1·000	15
QUADTREND + DCAPTIV	3·52	0·140	0·172	11
QUADTREND + RELSEAS	6·25	0·036	0·044	11
QUADTREND	10·55	0·004	0·005	10
QUADTREND + REPRO	12·44	0·002	0·002	11

Discussion

The Colorado lynx reintroduction programme is the largest Canada lynx, and one of the largest carnivore reintroduction programmes undertaken to date. Thus, evaluating this programme is important, and assessing the methods used may prove useful for other ongoing or future carnivore reintroductions (e.g. Iberian lynx *Lynx pardinus*, Amur leopard *Panthera pardus orientalis*, Barbary lion *Panthera leo leo*). Given the importance of adult survival in the dynamics of long-lived species (Dobson & Oli 2007), the long-term, high survival rates presented in this paper for the reintroduced lynx both inside (0·9315, SE = 0·0325) and outside (0·8219, SE = 0·0744) the reintroduction area are promising for the establishment of a viable population of lynx in Colorado.

Slough & Mowat (1996) found mortality in northern lynx populations to be strongly affected by the 10-year snowshoe hare cycle. This makes it difficult to directly compare annual survival rates of lynx across studies without knowing where each population is within this cycle. Further, it is possible the increased habitat fragmentation in the continental United States eliminates or dampens the amplitude of the snowshoe hare cycle in its southern distribution (Strohm & Tyson 2009), subsequently weakening the effect on demography of southern lynx populations. Nonetheless, our estimate of survival within the Colorado reintroduction area (0·9315 ± 0·0325) was higher than estimates obtained for natural, lightly trapped populations of Canada lynx in the Yukon (0·75–0·90, Slough & Mowat 1996; O'Donoghue *et al.* 1997) or in the Northwest Territories (~0·90, Poole 1994), where human disturbances are likely to be lower than in Colorado. Outside the study area, our estimate of survival was within the range estimated for the Kluane lynx population in south-west Yukon (O'Donoghue *et al.* 1997), and similar to the survival estimated for Eurasian lynx while accounting for hunting and poaching (Andrén *et al.* 2006).

According to Steury & Murray (2006) little human disturbance and from 1·1 to 1·8 snowshoe hares per hectare are required for a lynx population to be resilient. Given that few areas within the continental United States meet these criteria, they concluded that reintroductions of lynx would be unlikely to succeed. While other demographic parameters such as reproduction, recruitment and site fidelity must also be considered for fully evaluating the success of the reintroduction programme, we believe the results presented here are strongly encouraging and support the premise that Canada lynx reintroduction efforts can be successful in the continental United States.

We found that mortality was highest immediately after release and then decreased over the next 10–15 months, indicating an acute effect of the reintroduction itself (Fig. 3). This effect was most likely to be related to the stress induced by capture in the wild, transportation to Colorado, captivity, and release in a new environment. In addition, lynx are solitary and territorial, but multiple lynx (n = 12–55) were released in the area each year. Intraspecific competition may have occurred during this acclimation and exploration phase, leading to higher stress levels and territorial disputes, thus contributing to an acute effect on mortality.

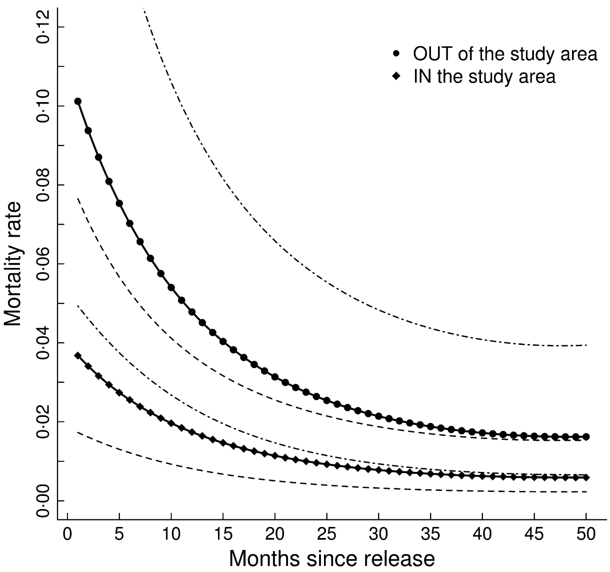

Fig. 3. Variation of monthly mortality rate with time since release for Canada lynx *Lynx canadensis* reintroduced to Colorado, inside and outside of the study area, according to our best-AIC$_c$ model {QUADTREND+RELYR}. Only the first 50 months following release are shown.

Under the final release protocol, lynx were held in captivity and fed a high quality diet for a minimum of 3 weeks before release. Thus, they were released in good body condition and one could expect that the longer the captivity, the lower the post-release mortality. Alternatively, there was concern that prolonged captivity could cause reintroduced lynx to associate humans with food and to seek them out for supply, thus increasing the risk of human-caused mortality. In the second best-AIC$_c$ model, post-release mortality decreased with time in captivity, but the effect was small and the 95% confidence interval overlapped zero. Based on this analysis, the number of days in captivity before release was not an important predictor of the variation in mortality. However, when focusing only on the first year post-release, Devineau *et al.* (unpublished data) found that mortality decreased when lynx were held captive for at least 5–6 weeks.

One could also expect a difference in survival between sexes, because males may wander more than females, or because males engage more in intraspecific competition (T. M. Shenk, unpublished data). However, sex was not an important predictor for variation in mortality [beta value for females: −0·0315, CI (−0·4415, 0·3786)]. We also found weak evidence that mortality varied with year of release, but this may be better explained by time-varying environmental factors not evaluated here rather than a specific release year effect.

Based on Byrne (1998), the reintroduction area was designated to encompass the largest, predicted, contiguous area of lynx-suitable habitat. Outside this area, suitable habitat was interspersed with unsuitable habitat, and fragmented by human infrastructures. We expected reintroduced lynx to first establish in the reintroduction area, then to colonize other suitable areas throughout Colorado. In fact, 82% of reintroduced lynx moved off the study area at least once, but the probability of an individual returning to the reintroduction area was slightly higher than for an individual to leave the area. This result, together with the lower mortality inside the reintroduction area, provides support for Byrne's (1998) assessment that the south-west quadrant of Colorado contains high quality habitat. Outside the reintroduction area, where habitat is more fragmented, lynx would have encountered more roads and opportunities for interactions with humans, hence increased human-related mortality. Further, the main causes of known mortality were vehicle collision and shooting, with more such deaths outside the study area (Table 2), although 36% of deaths could not be attributed to any cause.

Our multistate analysis strategy allowed us to estimate movement and mortality separately, as well as to incorporate imperfect detection probabilities. Such flexibility is not allowed by traditional telemetry analysis methods such as known fate (White & Garrott 1990) or nest survival (Schwartz *et al.* 2006) models. Animals regularly moved on and off the area of interest with little predictability, and with varying opportunities for detection. Reintroduced animals were fitted with tracking transmitters prior to release, not once they showed fidelity to the study area. In addition, the strong dispersal capability of the species is well documented (Mowat, Poole & O'Donoghue 1999), and was observed in Colorado (movements up to 1400 km, Fig. 1). Without our modelling approach, we would have estimated overall mortality directly after release to be 1·3 times higher than that found within the reintroduction area. This would have contributed to an overly pessimistic assessment of the reintroduction programme.

In our analysis, we could not distinguish between prolonged non-detection and collar loss/failure. Therefore, within the theoretical life expectancy of the transmitter, but in absence of a signal for > 3 months we coded missing data as a '.' (period), which were ignored in the analysis, potentially leading to underestimating mortality rates. We could have coded these missing data as zeros, but this could have lead to overestimation of mortality if a transmitter failed prematurely, or if collar failure coincided with the death of the lynx (e.g. collar destroyed in vehicle collision). We believe this uncertainty was greatest for 19 lynx located outside the study area and outfitted with VHF-only collars. However, when we coded these missing data with up to 60 zeros (i.e. the life-expectancy of VHF transmitters) our mortality estimates did not change to the hundredths place.

Carnivore reintroduction is considered to be an appropriate conservation strategy to restore the integrity of ecosystems. In Europe for example, there is a call for the release of more Eurasian lynx *Lynx lynx* and for increased monitoring (von Arx *et al.* 2004). Our results suggest general recommendations for future reintroductions of lynx, or of other carnivores. First, we believe it is important to identify a high-quality reintroduction area where mortality will be minimized. However, data collection and analyses should account for movements and demography of animals outside the reintroduction area. This seems especially true for wide-ranging, territorial animals. A reintroduction design should also recognize that mortality is likely to be higher shortly after release due to an acute reintroduction effect and that Canada lynx (and other carnivores) are likely to travel widely, leading to additional losses, hence requiring the release of more animals to achieve the desired density.

Acknowledgements

We thank W. Kendall and K. Burnham for suggestions during the analysis. We thank D. Freddy, M. Hebblewhite, D. Johnston, D. Martin, J. Squires and four anonymous reviewers for their comments which greatly improved the manuscript. The Colorado lynx reintroduction program involves many people in Canada and USA, all of whom deserve our thanks. CDOW personnel who played key roles include: J. Mumma, former director, W. Andree, G. Byrne, B. Gill, D. Kenvin, T. Malmsbury, J. Olterman (deceased), J. Seidel, S. Wait, M. Wild and L. Wolfe. We thank H. Dieterich and S. Dieterich for their dedication at the Frisco Creek Rehabilitation Center. Pilots D. Dhabolt, L. Gepfert, A. Keith, J. Olterman (deceased), M. Secor, B. Smith, W. Wannamaker, S. Waters, and D. Younkin performed hundreds of flights. T. Spraker conducted all necropsies. Research Associates R. Dickman and G. Merrill provided leadership in field data interpretation and collection with dedicated field crews (1999–2007). Funding was provided by CDOW, Great Outdoors Colorado (GOCO), Turner Foundation, USDA Forest Service, Vail Associates and the Colorado Wildlife Heritage Foundation.

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Received 24 July 2009; accepted 6 March 2010
Handling Editor: Mark Hebblewhite